

AGE VALIDATION OF THE COMMON THRESHER SHARK (*Alopias vulpinus*) IN
THE NORTHEASTERN PACIFIC OCEAN

A Thesis

by

NATALIE SPEAR

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Chair of Committee,	R.J. David Wells
Committee Members,	Bernd Würsig
	Hui Liu
Head of Department,	Anna Armitage

August 2017

Major Subject: Marine Biology

Copyright 2017 Natalie Spear

ABSTRACT

The purpose of this study was to validate the vertebral band pair deposition rate for Common Threshers (*Alopias vulpinus*) in the northeastern Pacific Ocean (NEPO). Vertebrae of 37 Common Threshers marked with oxytetracycline (OTC) were collected from tag-recapture efforts and used in this study. OTC tagging occurred off southern California from 1998 through 2013, and time at liberty of the 37 sharks ranged from 0.53 to 3.81 years with an average of 1.27 years (± 0.15 standard error, SE). Shark size at time of injection with OTC ranged from 63 to 128 cm fork length (FL) and from 83 to 168 cm FL at recapture. Vertebral band pair counts distal to the OTC marks indicate one band pair (1 translucent and 1 opaque) form annually for Common Threshers of the size range examined in the NEPO. This finding supports previous age and growth assumptions that have formed the basis of management decisions for the Common Thresher, and will support population dynamics data analyses moving forward.

DEDICATION

This thesis is dedicated to our capacity to choose kindness, compassion, and love, even —and perhaps especially — in our scientific endeavors, as individuals within the scientific community, and as part of the interconnected web of life. When it is by interacting with creatures that lets us explore, learn, thrive, and grow as individuals and as professionals, let us remember kindness and reverence for these and all beings. As we work to understand these animals, populations, and ecosystems: may we handle them as gently as possible, and may we make compassionate choices that serve their unencumbered and painless existence as individuals within their population, as part of an ecosystem, integral to the interconnected web of life.

ACKNOWLEDGEMENTS

I thank my entire committee and chair for their support, including R.J. David Wells (Chair), Suzanne Kohin, Bernd Würsig, and Hui Liu. This thesis would not be possible without members of the fishing community who participated in data and sample collection efforts including Capt. Tim Athens, National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center's (SWFSC) Highly Migratory Species Group, and the Shark Biology and Fisheries Science Lab at Texas A&M University at Galveston. Thank you to Tom TinHan, Kaylan Dance, Carlos Ruiz, Mike Kinney, Jeff Pulver, Sue Smith, Lisa Natanson, Brian Gervelis, Dovi Kacev, and Mike Dance for their expertise, assistance, and technical and moral support. Deep gratitude to Azure Lea, Alisa Zych, Mary Brechtel, Laura Mitchell (FG) Ph.D., Reynout Adrianus Roland-Holst DVM, and Scrappy for their amazing support, comic relief, and inspiration.

To the Common Thresher sharks who are central to this study—thank you does not feel appropriate, and it feels equally inappropriate to not acknowledge you here; may this work in some way contribute to the health of your former population and ecosystem.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Professor R.J. David Wells, PhD (Chair); Professor Hui Liu PhD; and Professor Bernd Würsig, PhD of the Department of Marine Biology and Suzy Kohin, PhD of the National Oceanic and Atmospheric Administration's National Marine Fisheries Service.

Fishery data and biological samples were provided by Suzy Kohin. Kaylan Dance, Tom TinHan, and Michael Bradley, contributed to sample processing.

All other work conducted for the thesis was completed by Natalie Spear independently.

Funding Sources

Graduate study and thesis research were supported by a research assistantship funded by Texas A&M University, NOAA SWFSC, with scholarships from the Houston Big Game Fishing Club and Texas A&M University's Conflict & Development/Applied Biodiversity Science Program.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
DEDICATION	iii
ACKNOWLEDGEMENTS	iv
CONTRIBUTORS AND FUNDING SOURCES.....	v
TABLE OF CONTENTS	vi
1. INTRODUCTION.....	7
1.1 Introduction (Specific)	12
2. MATERIALS & METHODS.....	16
2.1 Methods: Tagging	16
2.2 Methods: Age validation	18
2.2.1 Vertebrae sample preparation.....	18
2.2.2 Methods: Age validation - band pair counts	20
2.3 Methods: Thresher length.....	22
3. RESULTS.....	25
3.1 Results: Tag and recaptured oxytetracycline-marked Common Threshers	25
3.2 Results: Age validation	25
3.3 Results: Thresher length.....	26
4. DISCUSSION AND SUMMARY	28
REFERENCES	33
APPENDIX A: FIGURES	44
APPENDIX B: TABLES	54

1. INTRODUCTION

The Common Thresher, *Alopias vulpinus* (P.J. Bonnaterre, 1788) is a cartilaginous chordate. Together, the Common Thresher, Pelagic thresher (*Alopias pelagicus*; H. Nakamura 1935), and Bigeye Thresher (*Alopias superciliosus*; R. T. Lowe, 1841) comprise the genus *Alopias*, the singular genus within the Alopiidae family. The Alopiidae family falls in the order Lamniformes (a group also known as the mackerel sharks), within the subclass Elasmobranchii in the class Chondrichthyes. All three members of the genus *Alopias* are listed by the International Union for Conservation of Nature (IUCN) as *vulnerable*, due to declines in threshers globally (Goldman et al. 2009). All three species are categorized as *highly migratory species* by the United Nations Convention on the Law of the Seas (UN General Assembly 1982). In this thesis, the term Common Thresher will be used to refer to *A. vulpinus*.

The Common Thresher is found in epipelagic neritic and oceanic waters in the Atlantic, Pacific, and Indian Oceans, and the Mediterranean Sea (Compagno 2001). In the northeastern Pacific Ocean (NEPO, also referred to as Eastern North Pacific (ENP) in other studies) the Common Thresher migrates northerly and shoreward in warmer months (Moreno et al. 1989). The Southern California Bight (SCB), located within the California Current Large Marine Ecosystem (CCLME) in the NEPO; provides important habitat for neonates and juveniles found in nursery habitat close to shore (Cartamil et al. 2010, Cartamil et al. 2016). Larger juveniles, subadults, and adults are captured by the California Drift Gillnet (CADGN or DGN) fishery more frequently in offshore waters (Cartamil et al. 2010, Cartamil et al. 2016).

Fecundity and maturity estimates vary for Common Thresher studies across their range (Goldman 2005) and life history information is currently limited (Natanson & Gervelis 2013). The Common Thresher has an ovoviviparous mode of reproduction with oophagy (Natanson & Gervelis 2013, Gubanov 1972), also described in the literature as oophagous aplacental viviparity (Gilmore 1993, Moreno et al. 1989, Smith et al. 2008a). Oophagy is a shared trait among Lamniformes when fertile eggs are retained in the oviducts until embryos hatch, at which point they continue to develop while consuming infertile eggs supplied by the mother. Generally, Common Threshers give birth to 2-4, and most commonly 2 pups per clutch, though Moreno et al. (1989) documented up to 7 pups per brood in Spanish waters. Birth occurs seasonally in the spring months in both the NEPO and in the northeastern Atlantic Oceans (Moreno et al. 1989, Bedford & Haugen 1992) and on an annual cycle (Bedford & Haugen 1992) after an estimated gestation of 9 months (Goldman 2005).

Based on the von Bertalanffy growth model, Cailliet et al. (1983) estimated size at birth of Common Thresher at 158 cm total length (TL). Bigelow and Schroeder (1948) reported free swimming fetuses 117-120 cm TL, and Moreno et al. (1989) found term fetuses up to 159 cm TL. A 137 cm TL free swimming Common Thresher was reported in the western Indian Ocean (Compagno 2001), which suggests that either regional differences exist, or further data throughout the range is needed. The most recent estimate for Common Thresher age at maturity in the NEPO is 5.3 years and 4.8 years for females and males, respectively, (Smith et al. 2008b) though this data set did not include animals larger than approximately 250 cm FL. The Smith et al. (2008b) age and

growth study provided an update to the 1983 Cailliet et al. study in the same region (which found $K=0.108$, using an updated AL conversion equation and additional samples, nullifying the earlier Cailliet et al. (1983) findings (S.E. Smith, Seiurus Consulting, 2016, pers. comm.)). Common Threshers included in the current study primarily represent individuals through the juvenile stage, based on size at age estimates determined by Natanson & Gervelis (2013) and Natanson et al. (2016).

While Common Threshers have a circumglobal distribution, recovery rates after sharp declines suggest that there are multiple isolated subpopulations throughout the species range (Goldman et al. 2009). The fishery for Common Threshers off the US West Coast has been well documented since its inception in the late 1970s when it began as an experimental fishery in which gill nets, set nets, and longlines were used. In 1977, a targeted drift gillnet Common Thresher fishery in the region began with 15 commercial vessels, and grew to more than 225 vessels by 1982 (Hanan et al. 1993, Goldman 2005), referred to herein as the CADGN fishery. Due to a high market value for the species, the fishery switched to target Swordfish (*Xiphias gladius*) by the early 1980s. In 1982, the fishery peaked with a maximum reported landing of 1,089.5 metric tons of Common Thresher, which declined to fewer than 300 metric tons by the late 1980s (Maguire et al. 2006). Juvenile and subadult Common Threshers off central and southern California were less common in catches by the mid-1990s, and Common Thresher catches off California were reduced to 20% of formerly documented catch totals (Smith et al. 1998, PFMC 2013). A decrease in the number of Common Threshers caught was partially due to a reduction in fishing effort, and likely also due to a decrease in population size. In

1990, restrictions implemented to protect marine birds and mammals had severely limited the use of gillnets in the region (Smith et al. 1998, Maguire et al. 2006), which in turn significantly reduced fishing pressure and subsequent catch of the Common Thresher. Common Threshers tagged in the SCB are often subjected to fishing pressures from Mexico and the US (Cartamil et al. 2010, Cartamil et al. 2011, Hanan et al. 1993, O'Brien & Sunada 1994, Gonzalez 2008). Transboundary movements leave the Common Threshers vulnerable to fishing pressures in Mexican waters and in US waters where they are targeted by recreational anglers and are a valuable market species for commercial fishers.

Two factors are associated with the decline in Common Thresher catch. These include the effects of harvest pressure on the population and time area-closures that reduced fishing effort in the region. An assessment by Goldman et al. (2009) represents the IUCN position on Common Thresher status and asserts that DGN fishing pressures caused a significant decline in Common Threshers off central and southern California, evidenced in part by a decrease in mean length during the years 1981-1994 (Holts et al. 1998). However, the 2006 and 2012 HMS SAFE Reports (PFMC 2007b, PFMC 2013) state that recent low levels of Common Thresher catch were due to a reduction in catch effort in the region. The Pacific Fisheries Management Council (PFMC) Fishery Management Plan for U.S. West Coast Fisheries for Highly Migratory Species (PFMC 2007a) attributes the drop in Common Thresher catch per unit effort CPUE in the 1980s to high fishing pressure and catch in the DGN fishery. After the dramatic depletion in Common Thresher numbers in the 1990s, the Common Thresher population took longer

to recover than anticipated (Smith et al. 1998). Cortés (2008) observed that if elasticity and resiliency estimates had utilized the revised growth data from Smith et al. (2008b), recovery rates may not have been underestimated.

Validation of band pair deposition rates for Common Threshers in the region will increase confidence and perhaps accuracy in growth and resiliency analysis (Cortés 2008). Without a validated band pair deposition rate for the Common Thresher, existing growth curves (Cailliet et al 1983, Smith et al. 2008b, Teo et al. 2016) and related management strategy rely on band pair deposition rate assumptions and are built on a significant degree of uncertainty. The Pacific Fisheries Management Council (PFMC) lists data gaps in age and growth rates, maturity and reproductive schedules for the Common Thresher among the Council's most important research priorities (PFMC 2013). This thesis addresses this data gap and will contribute toward some of the highest research priorities and data needs among those identified by the PFMC (PFMC 2013).

A note on the terminology used in this paper, throughout the body of literature that supports this work, and that which this paper will likely support: At times the lexicon reflects the lens of a utilitarian value of these animals. *Stock* and *management*, are examples of words that set a utilitarian cognitive frame about the human relationship with the animals who are central to the study. This work is intended to support scientifically defensible sustainable management *of human activity* related to the killing and protection of *A. vulpinus*, with an implicit understanding of the intrinsic value of all life, including the lives of individual Common Thresher, in addition to their population and ecosystem level value.

1.1 Introduction (Specific)

The Common Thresher is an epipelagic mesopredator that inhabits neritic and oceanic waters in the Atlantic, Pacific, and Indian Oceans, and the Mediterranean Sea (Compagno 2001). In the northeastern Pacific Ocean (NEPO), the northeastern Atlantic, and western north Atlantic Ocean (WNA), the Common Thresher migrates northerly and shoreward in warmer months (April-August) (Moreno et al. 1989). Within the NEPO lies the California Current Large Marine Ecosystem (CCLME), home to the Southern California Bight (SCB). The SCB extends from 32°N (just south of the US-Mexican border) to Point Conception at 34.5°N, and encompasses waters that lie between 117°W to approximately 121°W. Tagging studies show juvenile and adult Common Threshers often associate with characteristically green, highly productive water, which correlates with upwelling and intense mixing (Cartamil 2009, National Marine Fisheries Service (NMFS) unpublished data) within the region. Common Threshers are more frequently found in coastal, shallow areas (Compagno 2001) of the SCB; however, they do occur farther offshore (generally within 65-120 km of land), particularly as they increase in size.

Multiple studies within the NEPO over in the past decade have revealed substantial information about Common Thresher life history and fishery interactions within the SCB-Baja California region (Aalbers et al. 2010, Bernal & Sepulveda 2005, Sepulveda et al. 2005, Cartamil 2009, Cartamil et al. 2010, 2011, and 2016, Cortés 2008, Sepulveda et al. 2015, Smith et al. 2008b). The highest known concentrations of the Common Thresher within the NEPO are found in the SCB (Cartamil et al. 2011, Hanan

et al. 1993). In the NEPO, satellite tag data show a southerly migration to warmer waters in the winter months (Cartamil et al. 2010, Smith & Aseltine-Neilson 2001). An area that is recognized to provide nursery resources for Common Threshers extends from the coastal region of the northernmost point of the SCB south to Sebastián Vizcaíno Bay, Baja California, Mexico (Cartamil 2009, Cartamil et al. 2010, 2016). These sharks tend to remain deeper during daylight hours, moving closer to the surface at night (Cartamil et al. 2010, 2016, Heberer et al. 2010).

The movement patterns of Common Threshers (and Blue Sharks (*Prionace glauca*), and Shortfin Mako Sharks (*Isurus oxyrinchus*)) tagged in the SCB leave them vulnerable to fishing pressures from both Mexico and the US (Cartamil et al. 2010, Cartamil et al. 2011, Gonzalez 2008, Hanan et al. 1993, and O'Brien & Sunada 1994). Satellite and conventional tag data demonstrate transboundary movement patterns, though little is known about the structure and dynamics of this population. The Pacific Fisheries Management Council (PFMC) lists data gaps in age and growth rates, maturity and reproductive schedules for the Common Thresher as highest research priorities (PFMC 2013).

The average age at first maturity is one of the most influential parameters in determining a shark population's resilience to harvest pressures and can be an indicator of ability to rebound from exploitation (Cortés 2002, Smith et al. 1998). Accurate determination of age-at-length values is necessary for growth and mortality rate calculations, in addition to longevity and age at recruitment (Campana 2001, Pardo et al. 2013). An important step in obtaining these values is to conduct age validation studies

using tagging techniques to determine the temporal significance of physiologic structures (bands) found on shark vertebrae. Once this validation is complete, vertebrae samples from unmarked (not injected with OTC) Common Thresher will be useful tools to determine the age-class structure of the population.

The rate at which band pairs are formed on the centrum is not uniform across shark species, and can vary within a species among geographic locations, and/or by age class (Natanson et al. 2016, Pratt & Casey 1983, Wells et al. 2013). Accurate age and growth data are essential for accurate resiliency and rebound estimates (Cortés 2008), which is essential for both single stock and ecosystem-based management. Studies have shown annual band pair deposition for the Lemon Shark, *Negaprion brevirostris* (Gruber & Stout 1983), Leopard Shark, (*Triakis semifasciata*) (Smith 1984), Porbeagle Shark (*Lamna nasus*) (Natanson 2002), and Blue Shark (Wells et al. 2017). Biannual deposition rates have been found for the juvenile Shortfin Mako Sharks in the NEPO (Wells et al. 2013) and WNA (Pratt & Casey 1983) and for the Scalloped Hammerhead (*Sphyrna lewini*) in northeastern Taiwanese waters (Chen et al. 1990) and off central Mexico in the NEPO (Anislado-Tolentino et al. 2008).

Published age and growth curves for the Common Thresher in the NEPO are based on the assumption of a one band pair per year deposition rate. The von Bertalanffy growth curves for Common Threshers off the US Pacific coast as determined by Smith et al. (2008b) assumed an annual band pair deposition rate throughout the lifespan of this species. A validation study of band pair deposition rate in the NEPO is necessary and important information to verify previous estimates of productivity and for development

of effective management strategies for this species. The purpose of the current study was to validate the vertebral band pair deposition rate for Common Threshers (*Alopias vulpinus*) in the NEPO.

2. MATERIALS & METHODS

2.1 Methods: Tagging

In 1982, the California Department of Fish and Game (CDFG) initiated an angler based shark tagging program. In 1998, the National Marine Fisheries Service (NMFS) initiated a thresher shark research program that included fishery-independent surveys and tagging studies on the Common Thresher. From 1982 to 2015, more than 2500 Common Threshers were tagged by CDFG, recreational anglers and NMFS, 1574 injected with OTC, and vertebrae samples that were attributed to 61 unique OTC-injected animals have been returned to NMFS after recapture by fishers. Additionally, hundreds of unmarked, untagged Common Thresher vertebrae have been collected by the NMFS Southwest Fisheries Science Center (SWFSC) along with length, sex, and maturity data through opportunistic sampling and via the drift gillnet and set net fishery observer program.

All of the thresher sharks tagged with OTC were released during NMSF fishery-independent shark surveys. Tagging efforts for the NMFS surveys occurred during the summer and fall months. The juvenile Common Thresher-targeted survey began in 2006 and operated September-October on 18 consecutive days using 12/0 or 13/0 circle hooks baited with Anchovy (*Engraulis mordax*), Sardine (*Sardinops sagax*), or Pacific Mackerel (*Scomber japonicus*), and focused on shallow (<46 m) nearshore sampling areas. Hooks were set on one or two 1.6 km longlines per station. When two replicate lines were used, they were set 0.4-0.8 km apart, each with approximately 100 hooks placed 15.24 m apart, and soaked 2-3 hours. A second NMFS longline survey operated

June-August also contributed to the data set for this study beginning in 1998, but primarily caught Juvenile Shortfin Mako and Blue Sharks. This survey operated within 80.4 km of shore in deeper water than the Common Thresher-targeted survey and occurred in mid- to late- summer 1998-2015.

When captured during a NMFS survey, Common Threshers were brought onboard using a cradle and kept oxygenated using a flow-through seawater hose fit with a PVC mouthpiece; a steady stream of seawater flowed across the gills from inside the mouth. Morphometric data collection including the straight-line distance from snout tip to the fork of the caudal fin (fork length, FL to the nearest cm) and a DNA sample were taken, a conventional tag was attached to the dorsal musculature, and an intraperitoneal injection of OTC was administered. When OTC was injected (at a dose rate of 25mg/kg body weight), a Rototag (Dalton ID, Henley-on-Thomas, UK) was affixed to the first dorsal fin. The Rototag included a unique identifier and a contact address for the tagging program, along with sampling instructions in English and Spanish. All animals marked with a unique ID by use of a conventional (also known as a *dart* or *spaghetti* tag) are referred to hereafter as *tagged*, whether or not the animal was also injected with OTC

The success of the tag-recapture study relied on fishers who returned samples and tag information to NMFS. To communicate the need for samples and associated data, outreach efforts consisted of meetings with fishery observers, fishers, seminars at fishing clubs, paper posters, and postings on online forums, explaining the reward program, compensation offered for the return of vertebral samples and catch information

on recaptured animals. These efforts informed commercial and recreational fishers about how to participate in and contribute to the research.

Upon capturing a Common Thresher tagged with a Rototag, it was requested that a vertebra (or multiple vertebrae) be collected from the spinal column, with geographic recapture location and length data and returned to the scientific team. Fishers were asked to return vertebrae extracted from the region just anterior to the caudal fin. However, the exact anatomic location of the vertebrae collected is neither identified by the sampler nor verifiable by the research staff. Gervelis and Natanson (2013) found vertebrae from any point along the vertebral column could be used for aging. The authors compared 6 entire vertebral columns from Common Threshers in the WNA and showed that while vertebrae radii decrease with proximity to the caudal fin and become more challenging to age, any vertebra is suitable, as counts along each column had a variance of at most 1 band pair. For the purposes of this study, we assume the same to be true for Common Threshers in the NEPO.

2.2 Methods: Age validation

2.2.1 Vertebrae sample preparation

A variety of techniques are used to prepare biological samples for assessment in age and growth studies. To determine the most effective technique for the preparation of Common Thresher vertebrae, the literature was consulted and a comparison of various techniques to elucidate bands appearing on the vertebral centrum face was completed. Techniques included the illumination of whole centrum faces using transmitted light and captured via digital photography, reflected light with digital photography, and the

staining of micro sections with Alizarin Red. Digital and film X-ray image techniques were also explored. The most effective method was found to be imaging with hard X-rays using a General Electric (Fairfield, CT) Mobile 100-15 X-ray unit.

For X-ray technique refinement, bowties cut along the frontal plane (Figures 1A and 1B) were the most effective for creating readable images of vertebral bands. The present study uses the term *frontal* to describe bowtie section orientation, which are cut along the frontal plane, intersecting and perpendicular to the sagittal plane. The following variables were modified to explore the optimal X-ray settings: thickness of bowtie cross section (0.5-1.5 mm), duration of exposure (5-55 seconds), a range of 1-5 milliamperes (mA), a range of 20-40 kilovolts (kV), and a variety of distances from sample to X-ray machine head (approximately 6 - 46 cm). Kodak Industrex M100 and Kodak Industrex M films were used (Readypack II; Eastman Kodak Co., Rochester, NY). Bowties with a 1 mm thickness placed 6-10 cm from the X-ray head, for 15-25 seconds at 5 mA and 35 kV, using either type of film produced the best image clarity and elucidation of banding patterns.

Table 1 shows observed minimum time necessary for OTC incorporation in vertebrae for multiple species. In the present study, returned vertebrae of threshers at liberty for 1 through 20 days showed fluorescence on the outer margin, though these marks did not appear as a cohesive, discernable ring. It is unclear at what point the OTC forms a cohesive discernable ring based on recapture specimens used in this study, or if this is consistent across individuals. A vertebra from a shark at liberty for 80 days exhibited a fluorescing OTC band distinct from the marginal tissue.

Samples were prepared for imaging using the methods of Natanson (2002) and Wells et al. (2013). A UV light was used to verify the existence of an OTC mark on each vertebral sample. Samples were selected for the study if a distinct OTC mark was visible and readable, and if the animal was at liberty at least 0.5 years before recapture. Once the mark was verified, excess tissue was removed from each vertebra, and samples were stored in ethanol. When several vertebrae were returned for the same animal, the largest vertebrae (other than the atlas and axis) were selected for the study and excess vertebrae were stored in a freezer without removing extra tissue for future use. Next, each vertebra to be used for the study was boiled in a beaker over low heat in water with a mild dish soap for several minutes to separate flesh from centrum. Vertebrae were then cleaned by hand with a toothbrush and dish soap. Two cuts were made, one on either side of the focus to create a section (approximately 1mm thick) along the frontal plane using a Beuhler IsoMet™ saw to create a bowtie. Each bowtie was then mounted on cardstock with super glue. Stainless steel pins were positioned and glued into place to indicate the location of the OTC mark, made visible through the use of a UV light and a dissecting microscope. X-rays of the bowties were made which yielded images showing contrast between regions of cartilage matrices of contrasting densities, termed bands. A lower density (hyaline) band and the distally adjacent higher density band are together called a band pair.

2.2.2 Methods: Age validation - band pair counts

Band pairs were counted by readers on digital images of X-ray photographs. If more visual detail was needed, the readers referred to the original X-rays. As in Bishop

et al. (2006) and Wells et al. (2013), counts started with the first band immediately after the birth band. The first band is always translucent, and the birth band represents age 0. Translucent bands (relatively hypomineralized; dark in standard (negative) X-ray images) and opaque bands (hypermineralized in comparison; appear light in standard (negative) X-ray images) alternate, and together represent one complete band pair. To ensure consistent counting methods, each of the three readers received a blank counting worksheet, a written protocol, and an illustrated guide. Reader counts were performed using a coding system to describe the band pattern and location of the OTC. Total number of bands after the birth band included the first band after the distal boundary of the birth band; which is always the first translucent zone after the birth band. A Leica® dissecting microscope with an Olympus® camera and cellSens® software were used to create digital images of the X-rays. When counting from the birth band toward the margin, band counts for post-OTC growth began at the distal boundary of the band which held the OTC mark, such that the band that contained the OTC mark was not included in the count. Total (post birth band) and post-OTC band counts included the marginal (centrum edge) band, whether translucent (less dense) or opaque (more dense), and regardless of band width (amount of tissue growth). Readers primarily used marks appearing on the corpus calcareum to distinguish bands. Patterns in the intermedialia were used to corroborate existence of a questionable band when section morphology and image quality allowed. Multiple images for each sample were provided to each reader and counted independently by 3 readers who did not have information related to sample ID number, shark length, sex, or time at liberty for the associated animal, or the size of

the centrum. Where readers disagreed on band counts, associated samples were assigned a new anonymizing sample name, placed in a random order by a 4th person who was not involved with vertebrae reading, and the 3 readers counted a second time. When readers agreed on the number of bands, counts were considered final. For samples readers did not agree on after two rounds of counting, the individual counts were subsequently averaged.

A least-squares linear regression analysis was performed to determine the band pair deposition rate. The null hypothesis was that the slope (b) of the relationship between the number of band pairs for each reader and time in years was 1:1 (if one opaque and one translucent band were deposited each year) was tested with a two-tailed t-test (Kusher et al. 1992). Age bias was investigated for readings after the OTC mark and after the birth band using age-bias plots and chi-square tests of symmetry using the contingency table methods of Bowker (1948) and Hoenig et al. (1995). The average percent error (APE) (Beamish and Fournier 1981) and average coefficient of variation (ACV, Campana et al. 1995; Chang 1982) were used to evaluate differences in reader counts; FISHMETHODS (Evans & Hoenig 1998) package in R, vers. 3.2.2 (R Development Core Team 2015) was used for these analyses.

2.3 Methods: Thresher length

Accurate length measurements of each shark at time of initial capture and recapture are necessary for the generation of accurate growth curves. While other length measurements were made for animals in the fishery observer data set, straight-line FL was used in this study as other measurements (e.g. total length (TL), standard length

(SL), alternate length (AL, straight-line distance from the origin of first dorsal to origin of second dorsal)) incur greater measurement inconsistencies. Length at tagging values include directly measured, estimated and converted lengths.

The following regression was calculated from 3069 records (mean=149.3 cm FL (57-283 cm FL) in the fishery observer data set (sexes combined, 1990-2015) to convert AL into FL, (Figure 2).

$$FL = 2.289(AL) + 21.392$$

$$r^2 = 0.87$$

The following equation was obtained using data collected during the fishery-independent NOAA Juvenile Shark and the Juvenile Thresher surveys and the fishery observer records 1982-2015. The equation was used to convert TL measurements to FL measurements when a recapture TL was provided but a recapture FL was not:

$$FL = 0.5274(TL) - 0.2269$$

$$r^2 = 0.998$$

The above linear regression was derived from 1112 records of animals (mean=130.9 cm FL; (57-253 cm FL); 561 females, 504 males, 47 unidentified) with FL and TL lengths measured directly (not estimated or converted) at time of tagging and during observed drift and set net fishing sets (Figure 3).

The Kolmogorov-Smirnoff test (*K-S*) is a goodness of fit test that tests the equality of distribution functions, and was used to determine if the length-frequency of male and female Common Threshers were similar and should be grouped together, and whether the fishery-independent and fishery observer data should be grouped. The *K-S*

test was performed on the subset of overall length data as described in the preceding paragraph. Additional *K-S* tests were performed separately on Common Threshers <150 cm FL, and ≥ 150 cm FL to determine if juvenile and/or mature threshers should be analyzed separately and by sex.

3. RESULTS

3.1 Results: Tag and recaptured oxytetracycline-marked Common Threshers

From 1982 to 2015, 2537 Common Threshers were tagged by NMFS and 1574 injected with OTC. A total of 105 thresher sharks were recaptured between 1983 and 2015 (Figure 4A). A total of 61 OTC-marked vertebral samples were returned, 37 of which were included in this validation study (Figure 4B). The remaining vertebrae samples were excluded due to a short time at liberty (<0.5 years), fluorescence appeared ambiguous or incohesive, or the vertebrae did not fluoresce. For the 37 OTC-marked sharks used in this study, average time at liberty was 462 days (± 55.5 SE), ranging from 192 to 1389 days. Average length was 99 cm FL (± 2.5 SE) at tagging and 123 cm FL (± 3.9 SE) at recapture. For females and males, the average length at tagging was 105 cm FL (± 3.1 SE) and 92 cm FL (± 3.6 SE), respectively and 132 cm FL (± 5.0 SE) and 113 cm FL (± 4.8 SE) at recapture. (Table 2).

3.2 Results: Age validation

Results from readings of the OTC-marked vertebrae in this study indicated that 1 band pair is deposited each year. The slope of the relationship between the number of band pairs deposited each year and years at liberty did not significantly differ from the 1:1 relationship ($P=0.47$; $P>0.05$); the predicted average number of band pairs deposited each year was modeled with the following linear regression (Figure 5):

$$(\text{Average band pairs post OTC}) = 0.8982(\text{years at liberty}) - 0.0569$$

$$r^2 = 0.75$$

Time at liberty, average number of band pairs observed after the OTC mark and after the birth band, and size at time of tagging and recapture are summarized in Table 2. A vertebra from a Common Thresher at liberty for 1389 days (3.81 years) with labeled band pairs is shown in Figure 6.

There were no significant differences among reader counts for band pair counts distal to the OTC mark (ANOVA; $P=0.998$) or among total counts distal to the birth band (ANOVA; $P=0.998$). Age bias was negligible: age-bias plots (Figure 7) and chi-square tests of symmetry showed that differences in reader counts showed no systematic bias ($P>0.05$). Variability among reader counts was low with an APE of 7.56% and an ACV of 9.86% for counts after the OTC mark and with an APE of 6.10%, and an ACV of 8.02% for counts distal to the birth band. Among readers, all of the final band pair counts after the OTC were within 1 band pair of each other, and 97% (36 of 37) of the counts after the birth band were within 1 band pair (Table 2).

3.3 Results: Thresher length

The length-frequency data set (which included a subset of all tagged Common Threshers) from 1983-2014 for fishery-independent and fishery observer data of Common Threshers in the region ranged from 36 to 283 cm FL, with an average length of 137 cm FL (± 0.39 SE). Box and whisker plots (Figure 8) separate frequencies by sex: male range was 36-256 cm FL, averaging 136 cm FL (± 0.56 SE); and the female range was 45-283 cm FL, with an average length of 138 cm FL (± 0.54 SE).

Length frequencies significantly differed by sex within the fishery observer and fishery-independent datasets (Figure 8). However, for the 60% of Common Threshers

that were <150 cm FL the two-sample *K-S* test supports combining sexes ($P = 0.38$, Figure 8). The average lengths of males and females in the combined fishery observer and fishery-independent data set were similar, with females showing greater lengths, Figure 8.

4. DISCUSSION AND SUMMARY

This was the first study to provide validation of the vertebral band pair deposition rate for the Common Thresher in the NEPO. It contributes to the value of existing age and growth literature and associated assumptions, provides a robust foundation for Common Thresher population age and growth studies moving forward, and provides information that can inform decisions about regulations that impact this population in the NEPO. With their relatively high trophic position (Estrada et al. 2003), Common Threshers play an important role in the ecosystem, and may exert strong top-down effects on their prey relative to other more generalist species, although more data is needed in this area (Young et al. 2016). As Common Thresher is a highly migratory species, the success of this project relied on cooperation and collaboration between fishers and researchers in the United States and Mexico to maximize tag, vertebrae and data recovery. Collaboration of this nature is necessary not only in biological sampling, but also in the implementation of management decisions moving forward.

The band pair deposition rate of one band pair per year found in the current study is consistent with Natanson et al.'s (2016) findings for Common Threshers in the WNA of the same size range and up to approximately 14 years of age (validated through bomb radiocarbon dating) and for several other elasmobranch species. Among these species are the Blue Shark (Wells et al. 2017), Leopard Shark (Smith 1984), Thornback Ray (*Raja clavata*) (Holden & Vince 1973), and the Diamond Stingray, *Dasyatis dipterura* (Smith et al. 2007). Due to the prevalence of the one band pair per year deposition rate

among elasmobranch species, it is often the assumed deposition rate for species without validated band pair deposition rates.

The band pair deposition rate found in the current study should be applied to Common Threshers less than or equal to the size range examined in this study. Natanson et al. (2016) found that band pair deposition rate may change over the lifespan of Common Threshers in the WNA, with an early life deposition rate of one band pair per year, up to approximately age 14, subsequently decreasing in deposition frequency. This observation led to an update to previously published growth curves for the species in the WNA. Additionally, studies on band pair deposition rates in other elasmobranch species have found band pair depositions rates can vary over the lifetime of the shark as in the case of the Sandbar Shark (*Carcharhinus plumbeus*), which demonstrate a predictable temporal rhythm of deposition before switching to a lack of periodicity later in life (Casey & Natanson 2002). For the Pacific Angel Shark, *Squatina californica*, Natanson (1984) found no apparent time-related periodicity of band pair formation. It was instead related to somatic growth rates and, in concurrence with Ridewood (1921), suggested the purpose of these bands is to support the structural integrity of the spinal column. A single band pair per year deposition rate was assumed for the Shortfin Mako in the NEPO, until a biannual band pair deposition rate for juvenile Shortfin Mako Sharks was found via OTC validation (Wells et al. 2013), with a transition to one band pair per year in males at about the size of maturity (Kinney et al. 2016). A biannual deposition rate has also been suggested for the Scalloped Hammerhead (*Sphyrna lewini*) by Chen et al. (1990) in northeastern Taiwanese waters and by Anislado-Tolentino et al. (2008) for

Scalloped Hammerheads off the southern coast of Sinaloa, Mexico, though a one band pair per year deposition rate for the same species off of the southern coast of Brazil was observed by Kotas et al. (2011).

With a size range of 63 cm FL (minimum length at tagging) to 168 cm FL (maximum length at recapture), the largest Common Threshers included in the study are estimated at 5 years of age based on the Smith et al. (2008b) von Bertalanffy estimate, and 6 years of age, based on the Schnute Growth model using parameters developed in the WNA by Natanson et al. (2016). Smith et al. (2008b) estimated maturity at 160 cm FL (303 cm TL) in the Pacific Ocean for both sexes combined, and the latest status review report for Common Threshers in the NEPO (Young et al. 2016) uses a 50% maturity rate for females in the NEPO at age 5 based on Smith et al. (2008a), and assumes maturity at >166 cm FL suggesting that at least one female was mature by the time of recapture in this age validation study. Natanson et al. (2016) found age at maturity (50%) to be 14 years for females and age 8 years for males (Natanson & Gervelis 2013, Natanson et al 2016). The Natanson et al. (2016) study suggests even the largest animals in the current study fall below the 50% maturity rate.

Sample A079055, a female recaptured at 168 cm FL (converted to 318 cm TL) had 5.0 total band pairs. Based on Smith et al. (2008b), females mature at 260–315 cm TL, at 3–4 years of age, suggesting that larger individuals such as A079055 and others included in the study may have been reproductively mature. The difference in size at age and size-at-maturity between the Smith et al. (2008b) and Natanson et al. (2016) studies may be due to ontogenetic differences among growth rates in the two regions, and

differences in data analysis protocol, and conversion equation differences. Length-type conversion equation differences between Smith et al (2008b) and Natanson & Gervelis (2013) may have contributed differences in size-at-maturity estimates. Further studies on maturity of Common Threshers may help explain these apparent differences between regions.

Future validation studies should include larger animals to more fully represent the range of sizes found within the fishery. A comprehensive understanding of Common Thresher age and growth in the NEPO will benefit from band pair deposition rate validation for larger animals. The largest Common Thresher included in the current validation study was 168 cm FL at the time of recapture, while fishery observer data in the NEPO includes animals up to 283 cm FL (Figure 8). As further validation of larger Common Threshers in the NEPO is undertaken, sexual dimorphism in larger size classes should be taken into account in growth rate and reproductive biology analyses. Due to time and area fishery closures implemented for the protection of reproductive females and for the protection of other species, samples of larger Common Threshers are limited in the NEPO, as the recapture of tagged animals is primarily opportunistic and dependent on fishing activity.

With a validated band pair deposition rate for Common Threshers in the NEPO, age and growth studies, stock assessments, and management decisions can benefit from more accurate age estimates. Future age validation studies in the NEPO should include larger animals to achieve a more complete assessment of band pair deposition rate throughout the Common Thresher lifespan. Further studies into size-at-maturity within

the NEPO will provide useful information about the age and growth of the Common Thresher when paired with the validated band pair deposition data in conjunction with age-at-length values that can be based on the validation study, and will provide greater certainty regarding potential ontogenetic differences between the NEPO and WNA Common Thresher populations.

REFERENCES

- Aalbers, S. A., Bernal, D., & Sepulveda, C. A. (2010) The functional role of the caudal fin in the feeding ecology of the Common Thresher shark *Alopias vulpinus*. *Journal of Fish Biology*, 76(7), 1863-1868.
- Anislado-Tolentino, V., Cabello, M. G., Linares, F. A., & Mendoza, C. R. (2008) Age and growth of the scalloped hammerhead shark, *Sphyrna lewini* (Griffith & Smith, 1834) from the Southern coast of Sinaloa, México. Edad y crecimiento del tiburón martillo, *Sphyrna lewini* (Griffith & Smith, 1834) de la costa sur de Sinaloa, México. *Hidrobiológica*, 18(1), 31-40.
- Beamish, R. J., & Fournier, D. A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, 38(8), 982-983.
- Bedford, D., & Haugen, C. W. (1992) Thresher shark. California's living marine resources and their utilization, WS Leet, CM Dewees, and CW Haugen, eds. California Sea Grant Publication UCSGEP-92-12, Davis, Calif, 49-51.
- Bernal, D., & Sepulveda, C. A. (2005) Evidence for temperature elevation in the aerobic swimming musculature of the Common Thresher shark, *Alopias vulpinus*. *Copeia*, 2005(1).
- Bigelow, G.W., & Schroeder W. C. (1948) Fishes of the western North Atlantic. Mem. *Sears Foundation for Marine Research at Yale University*, pp. 59–552.
- Bishop, S. D. H., Francis, M. P., Duffy, C., & Montgomery, J. C. (2006) Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus*

- oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research*, 57(2), 143-154.
- Bowker, A. H. (1948) A test for symmetry in contingency tables. *Journal of the American Statistical Association*, 43(244), 572-574.
- Branstetter, S. (1987) Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. *Copeia*, 964-974.
- Cailliet, G. M., Martin, L. K., Martin, J. T., Harvey, J. T., Kusher, D. and Welden, B. A. (1983) Preliminary studies on the age and growth of the blue, *Prionace glauca*, Common Thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. In: *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks* (eds. E. D. Prince and L. M. Pulos). NOAA Technical Report NMFS 8. NOAA/NMFS, Silver Spring, MD, pp. 1–17.
- Campana, S. E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, 59(2), 197-242.
- Campana, S. E., Annand, M. C., & McMillan, J. I. (1995) Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society*, 124(1), 131-138.

- Cartamil D. (2009) Movement patterns, habitat preferences, and fisheries biology of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Doctoral Dissertation, University of California.
- Cartamil, D., Santana-Morales, O., Escobedo-Olvera, M., Kacev, D., Castillo-Geniz, L., Graham, J. B. & Sosa-Nishizaki, O. (2011) The artisanal elasmobranch fishery of the Pacific coast of Baja California, Mexico. *Fisheries Research*, 108(2), 393-403.
- Cartamil, D., Wegner, N. C., Aalbers, S., Sepulveda, C. A., Baquero, A., & Graham, J. B. (2010) Diel movement patterns and habitat preferences of the Common Thresher shark (*Alopias vulpinus*) in the Southern California Bight. *Marine and Freshwater Research*, 61(5), 596-604.
- Cartamil, D., Wraith, J., Wegner, N.C., Kacev, D., Lam, C.H., Santana-Morales, O., Sosa-Nishizaki, O., Escobedo-Olvera, M., Kohin, S., Graham, J.B. and Hastings, P., (2016) Movements and distribution of juvenile Common Thresher sharks *Alopias vulpinus* in Pacific coast waters of the USA and Mexico. *Marine Ecology Progress Series*, 548, pp.153-163.
- Casey, J.G., and L.J. Natanson. (1992) Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 49:1474-1477.
- Chang, W. Y. (1982) A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*, 39(8), 1208-1210.

- Chen, C. T., Leu, T. C., Joung, S. J., & Lo, N. C. H. (1990) Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Pacific Science*, 44(2), 156-170.
- Compagno, L. J. (2001) *Sharks of the world: an annotated and illustrated catalogue of shark species known to date Volume 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO Species Catalogue for Fishery Purposes (Vol. 2, No. 1). FAO, Rome, Food & Agriculture Organization. 269 pp.
- Cortés, E. (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology*, 16(4), 1048-1062.
- Cortés, E. (2008) Comparative life history and demography of pelagic sharks. In: *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds. M. D. Camhi, E. K. Pikitch and E. A. Babcock). Blackwell Publishing Oxford, UK.
- Estrada, J. A., Rice, A. N., Lutcavage, M. E., & Skomal, G. B. (2003) Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *Journal of the Marine Biological Association of the UK*, 83(06), 1347-1350.
- Evans, G.T. and J.M. Hoenig. (1998) Testing and viewing symmetry in contingency tables, with application to readers of fish ages. *Biometrics* 54:620-629.
- Gervelis, B. J., & Natanson, L. J. (2013) Age and growth of the Common Thresher shark in the Western North Atlantic Ocean. *Transactions of the American Fisheries Society*, 142(6), 1535-1545.

- Gilmore, R. G. (1993) Reproductive biology of lamnoid sharks. *Environmental Biology of Fishes*, 38(1-3), 95-114.
- Goldman, K. J. (2005) Thresher Shark *Alopias vulpinus* (Bonnaterre, 1788). Pages 250–252 in S. L. Fowler, R. D. Cavanagh, M. Camhi, G. H. Burgess, G. M. Cailliet, S. V. Fordham, C. A. Simpfendorfer, and J. A. Musick, editors. *Sharks, rays and chimaeras: the status of the chondrichthyan fishes*. IUCN (The World Conservation Union), IUCN/SSC Shark Specialist Group, Gland, Switzerland.
- Goldman, K.J., Baum, J., Cailliet, G.M., Cortés, E., Kohin, S., Macías, D., Megalofonou, P., Perez, M., Soldo, A. & Trejo, T. (2009) *Alopias vulpinus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2016-3. www.iucnredlist.org. Downloaded on 20 March 2017.
- Gonzalez, E. (2008) Descripción de los movimientos del tiburón azul (*Prionace glauca*) usando telemetría satelital (Doctoral dissertation, MS Thesis. Centro de Investigación Científica y de Educación Superior de Ensenada, BC).
- Gruber, S. H., & Stout, R. G. (1983) Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks*. NOAA Tech Rep NMFS (Vol. 8, pp. 193-205).
- Gubanov, Y. P. (1972) On the biology of the thresher shark, *Alopias vulpinus* (Bonnaterre), in the northwest Indian Ocean. *Journal of Ichthyology*, 12(4), 591-600.

- Hanan D.A., Holts D.B., & Coan A.L. (1993) The California drift gillnet fishery for sharks and swordfish, 1981-1982 through 1990-1991. *Fishery Bulletin* 175:1-95.
- Heberer, C., Aalbers, S. A., Bernal, D., Kohin, S., DiFiore, B., & Sepulveda, C. A. (2010) Insights into catch-and-release survivorship and stress-induced blood biochemistry of Common Thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. *Fisheries Research*, 106(3), 495-500.
- Hoenig, J. M., Morgan, M. J., & Brown, C. A. (1995) Analysing differences between two age determination methods by tests of symmetry. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(2), 364-368.
- Holden, M.J. and M.R. Vince. (1973) Age validation studies on the centra of *Raja clavata* using tetracycline. *Journal Conseil International de l'Exploration de la Mer*, 35(1):13-17.
- Holts, D. B., Julian, A., Sosa-Nishizaki, O. and Bartoo, N. (1998) Pelagic shark fisheries along the west coast of the United States and Baja California, Mexico. *Fisheries Research*, 39, 115–125.
- Kinney, M. J., Wells, R. J. D. and Kohin, S. (2016) Oxytetracycline age validation of an adult shortfin mako shark *Isurus oxyrinchus* after 6 years at liberty. *Journal of Fish Biology*, 89(3), 1828-1833.
- Kotas, J. E., Mastrochirico, V., & Petre Junior, M. (2011). Age and growth of the Scalloped Hammerhead shark, *Sphyrna lewini* (Griffith and Smith, 1834), from the southern Brazilian coast. *Brazilian Journal of Biology*, 71(3), 755-761.

- Kusher, D. I., Smith, S. E., & Cailliet, G. M. (1992) Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environmental Biology of Fishes*, 35(2), 187-203.
- Maguire, J.J., Sissenwine, M., Csirke, J., Grainger, R., & Garcia, S. (2006) The state of world highly migratory, straddling and other high seas fishery resources and associated species. FAO Fisheries Technical Paper. No. 495. Rome, FAO. 84 pp.
- Moreno, J. A., Parajúa, J. I., & Morón, J. (1989) Biología reproductiva y fenología de *Alopias vulpinus* (Bonnaterre, 1788) (Squaliformes: Alopiidae) en el Atlántico nor-oriental y Mediterráneo occidental. *Scientia Marina*, 53(1), 37-46.
- Natanson, L. J. (2002) Preliminary investigations into the age and growth of the shortfin mako, *Isurus oxyrinchus*, white shark, *Carcharodon carcharias*, and thresher shark, *Alopias vulpinus*, in the Western North Atlantic Ocean. *International Commission for the Conservation of Atlantic Tunas Working Document*, Standing Committee on Research and Statistics, 1, 66.
- Natanson, L. J., & Gervelis, B. J. (2013) The Reproductive Biology of the Common Thresher Shark in the Western North Atlantic Ocean. *Transactions of the American Fisheries Society*, 142(6), 1546-1562.
- Natanson, L. J., Hamady, L. L., & Gervelis, B. J. (2016) Analysis of bomb radiocarbon data for common thresher sharks, *Alopias vulpinus*, in the northwestern Atlantic Ocean with revised growth curves. *Environmental Biology of Fishes*, 99(1), 39-47.

- O'Brien, J. W., & Sunada, J. S. (1994) A review of the southern California experimental drift longline fishery for sharks, 1988–1991. *CalCOFI Rep*, 35, 222-229.
- Pacific Fishery Management Council (2007a) *Fishery Management Plan for U.S. West Coast Fisheries for Highly Migratory Species*. Portland, OR: PPMC. June 2007.
- Pacific Fishery Management Council (2007b) Status of the U.S. West Coast Fisheries for Highly Migratory Species through 2006, Stock Assessment and Fishery Evaluation. Portland, OR: PPMC. September 2007.
- Pacific Fishery Management Council (2013) Stock Assessment and Fishery Evaluation (SAFE) HMS (Highly Migratory Species) Report, 2012. Portland, Oregon: PPMC. Available: http://www.pcouncil.org/wp-content/uploads/4.-StockStatus_2013.pdf. (Accessed April 2014).
- Pardo, S. A., Cooper, A. B. and Dulvy, N. K. (2013) Avoiding fishy growth curves. *Methods Ecol Evol*, 4: 353–360. doi:10.1111/2041-210x.12020.
- Pratt Jr, H. L., & Casey, J. G. (1983) Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 40(11), 1944-1957.
- R Development Core Team (2015) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ridewood, W. G. (1921) On the calcification of the vertebral centra in sharks and rays. *Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character*, 210, 311-407.

- Sepulveda, C A., Wegner, N C., Bernal, D., & Graham, J. B. (2005) The red muscle morphology of the thresher sharks (family Alopiidae). *Journal of Experimental Biology*, 208(22), 4255-4261.
- Sepulveda, C. A., Heberer, C., Aalbers, S. A., Spear, N., Kinney, M., Bernal, D., & Kohin, S. (2015) Post-release survivorship studies on common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. *Fisheries Research*, 161, 102-108.
- Smith, S. E. (1984) Timing of vertebral-band deposition in tetracycline injected leopard sharks. *Transactions of the American Fisheries Society*, 113: 308-313.
- Smith, S. E. (2004) *First year results: Thresher shark (Alopias vulpinus) nursery ground and pre-recruit index study, September 2003-September 2004*. National Marine Fisheries Service. SWFSC. Administrative report LJ-05-01.
- Smith, S. E., & Aseltine-Neilson, D. (2001) Thresher shark. *California's Living Marine Resources: a Status Report*. (Eds WS Leet, CM Dewees, R. Klingbeil and EJ Larson.) pp, 339-341.
- Smith, S. E., Au, D. W., & Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, 49(7), 663-678.
- Smith, S.E., Au, D.W. & Show, C. (2008a) Intrinsic rates of increase in pelagic elasmobranchs. In: *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds. M. D. Camhi, E. K. Pikitch and E. A. Babcock). Blackwell Publishing Oxford, UK.

- Smith, S. E., Rasmussen, R. C., Ramon, D. A. and Cailliet, G. M. (2008b) The biology and ecology of thresher sharks (Alopiidae). In: *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds. M. D. Camhi, E. K. Pikitch and E. A. Babcock). Blackwell Publishing Oxford, UK.
- Smith, W. D., Cailliet, G. M., & Melendez, E. M. (2007) Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura*. *Marine and Freshwater Research*, 58(1), 54-66.
- Tanaka, S. (1990) Age and growth studies on the calcified structures of newborn sharks in laboratory aquaria using tetracycline. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries*. National Oceanic and Atmospheric Administration, Technical Report, National Marine Fisheries Service, 90, 189-202.
- Teo, S.L., Rodriguez, E.G. & Sosa-Nishizaki, O. (2016) Status of common thresher shark along the west coast of North America. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFSC-557. Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California.
- UN General Assembly, Convention on the Law of the Sea, 10 December 1982.
- Wells, R. D., Spear, N., & Kohin, S. (2017) Age validation of the blue shark (*Prionace glauca*) in the eastern Pacific Ocean. *Marine and Freshwater Research*. Research doi:10.1071/MF16054.

Wells, D.R.J., Smith, S. E., Kohin, S., Freund, E., Spear, N., & Ramon, D. A. (2013)

Age validation of juvenile Shortfin Mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California. *Fishery Bulletin*, 111, 147-160.

Wilson, C.A., Brothers, E.B., Casselman, J.M., Smith, C.L., & Wild, A. (1983)

Glossary. *In* Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. NOAA Technical Report NMFS, 8, 207-208.

Young, C.N., Carlson, J., Hutchinson, M., Kobayashi, D., McCandless, C., Miller, M.H.,

Teo, S., and T. Warren. (2016) Status review report: Common Thresher shark (*Alopias vulpinus*) and bigeye thresher shark (*Alopias superciliosus*). Final Report to National Marine Fisheries Service, Office of Protected Resources. March 2016. 199 pp.

APPENDIX A:

FIGURES

- Figure 1: Vertebrae preparation a (A) anatomic planes of a fish, (B) oxytetracycline mark fluorescing under UV light; bowtie cut is made along the green line, the frontal plane (C) pin placement with UV light, (D) and X-ray image with pin indicating OTC location and bands elucidated. Image A is adapted from an image in Wilson et al. (1983).46
- Figure 2: Alternate length (AL) to fork length (FL) regression equation to convert alternate length (TL) to FL for the Common Thresher (*Alopias vulpinus*) in the northeastern Pacific. Regression equation is based on data collected from observers in the drift gillnet and set net fishery, 1990-2015, northeastern Pacific Ocean; $n = 3609$, $r^2 = 0.87$47
- Figure 3: Total length (TL) to fork length (FL) regression equation to convert TL to FL for the Common Thresher (*Alopias vulpinus*) in the northeastern Pacific Ocean. Equation was calculated based on measurements collected from the drift gillnet and set net fishery and from annual fishery-independent surveys in the Southern California Bight, northeastern Pacific Ocean (1990-2015), $n = 1112$ (504 males, 561 females), $r^2 = 0.998$48
- Figure 4: Maps showing tag and recapture locations for (A) all recaptured Common Thresher sharks (*Alopias vulpinus*) (1983-2015), $n = 105$ and (B) OTC tagged and recaptured Common Threshers whose vertebrae were used in this study ($n = 37$). Green dots are tagging locations and purple dots represent recapture locations.49
- Figure 5: Average number of vertebral band pairs after the oxytetracycline mark compared to days at liberty. Common Threshers (*Alopias vulpinus*) tagged and recaptured in the northeastern Pacific (1998-2013). Readings were determined by 3 independent readers (\pm standard error [SE]). The solid line represents the linear regression of band pairs relative to days at liberty. Animals at liberty ≥ 0.5 years are included, $n = 37$50
- Figure 6: Band pair progression in X-ray images of a vertebra section showing band pair progression of an OTC-marked Common Thresher (*Alopias vulpinus*) recaptured in the northeastern Pacific Ocean. Translucent cartilage (dark bands on image) contrasted with more densely mineralized cartilage tissue (appearing light on image) shown with a “o” symbol to indicate the location of an opaque bands.51
- Figure 7: Age-bias plots for 3 independent readers who aged all OTC-marked Common Thresher (*Alopias vulpinus*) vertebrae to determine number of

band pair counts distal to the OTC mark (left column) and total number of band pairs distal to the birth band (right column). No significant difference among band pair counts distal to the OTC mark (ANOVA; $P=0.998$) or among total counts distal to the birth band (ANOVA; $P=0.998$).52

Figure 8: Boxplots showing (A) length distribution of male ($n= 3985$, fork length (FL) = $136 (\pm 0.57 \text{ standard error [SE]})$, 36-256 cm) and female ($n= 4374$, FL = $138 (\pm 0.54 \text{ SE})$, 45-283 cm) Common Threshers and (B) average length of fishery-independent ($n= 2488$, FL = $106 (\pm 0.53 \text{ SE})$, 44-245 cm) and California drift gillnet and set net fishery observer data ($n= 5977$, FL = $149.5 (\pm 0.41 \text{ SE})$, 36-283 cm) 1990-2014. Y-axes represent shark size in cm FL.....53

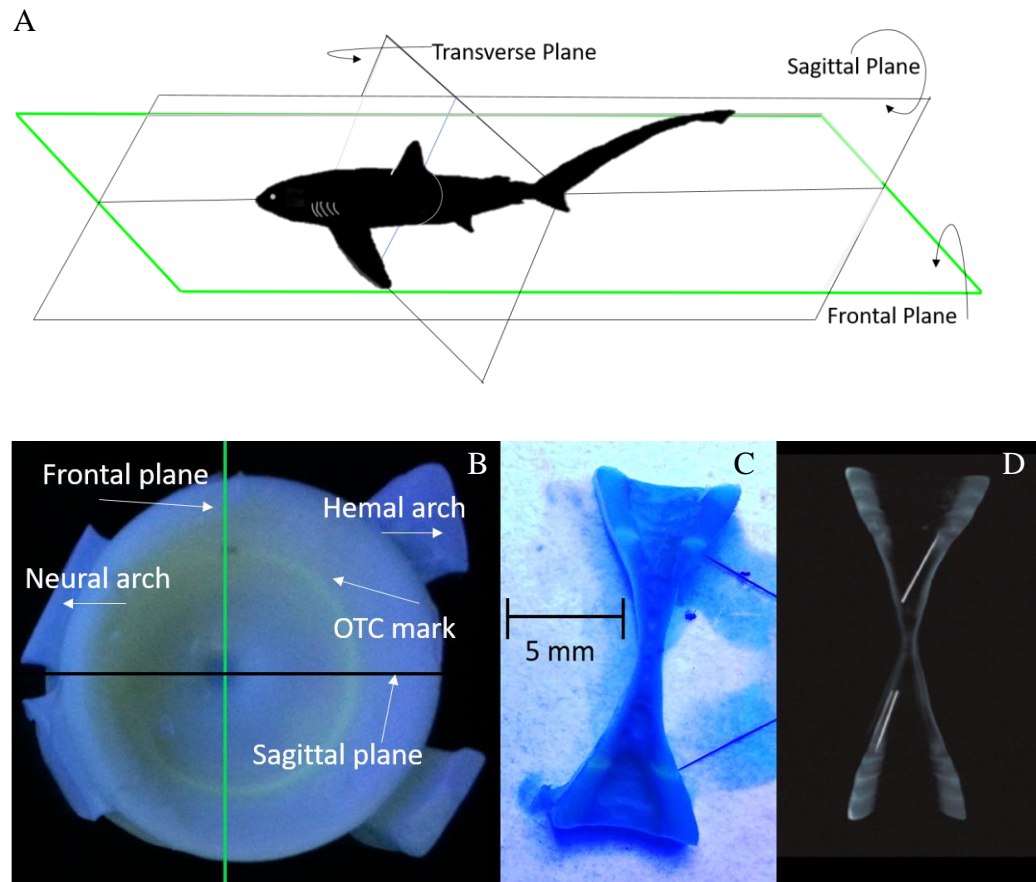


Figure 1: Vertebral preparation a (A) anatomic planes of a fish, (B) oxytetracycline mark fluorescing under UV light; bowtie cut is made along the green line, the frontal plane (C) pin placement with UV light, (D) and X-ray image with pin indicating OTC location and bands elucidated. Image A is adapted from an image in Wilson et al. (1983).

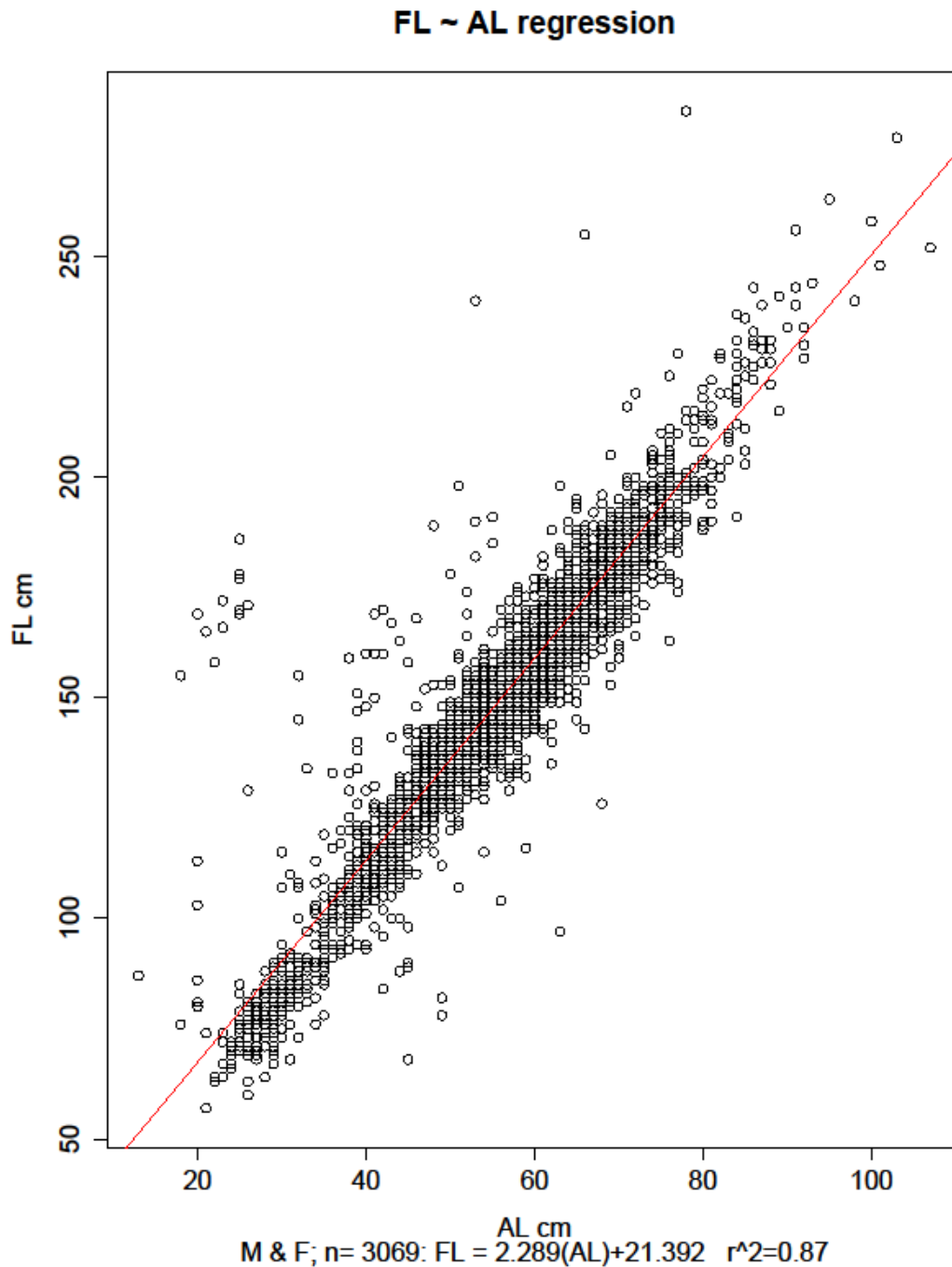


Figure 2: Alternate length (AL) to fork length (FL) regression equation to convert alternate length (TL) to FL for the Common Thresher (*Alopias vulpinus*) in the northeastern Pacific. Regression equation is based on data collected from observers in the drift gillnet and set net fishery, 1990-2015, northeastern Pacific Ocean; n= 3609, $r^2=0.87$.

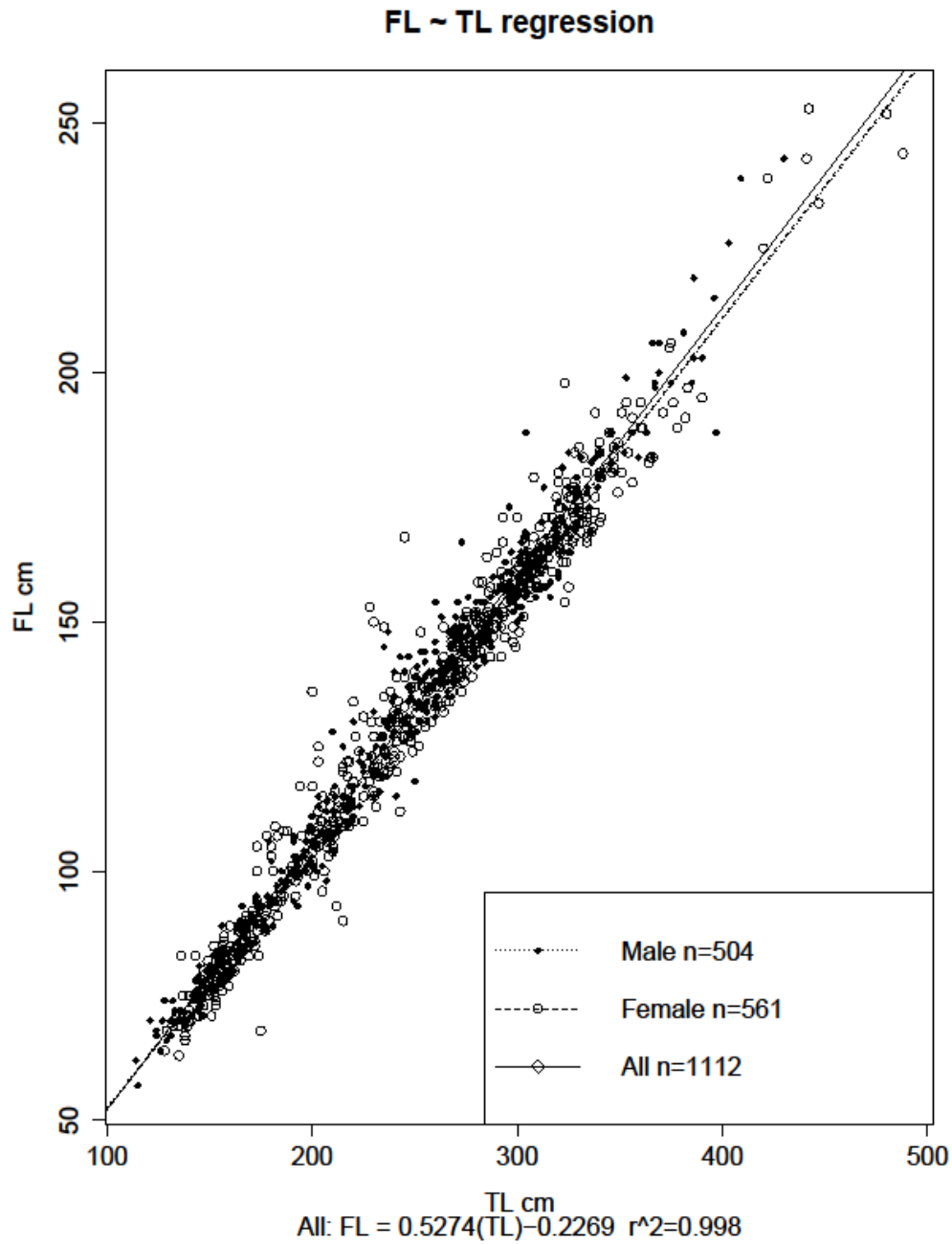


Figure 3: Total length (TL) to fork length (FL) regression equation to convert TL to FL for the Common Thresher (*Alopias vulpinus*) in the northeastern Pacific Ocean. Equation was calculated based on measurements collected from the drift gillnet and set net fishery and from annual fishery-independent surveys in the Southern California Bight, northeastern Pacific Ocean (1990-2015), $n = 1112$ (504 males, 561 females), $r^2 = 0.998$.

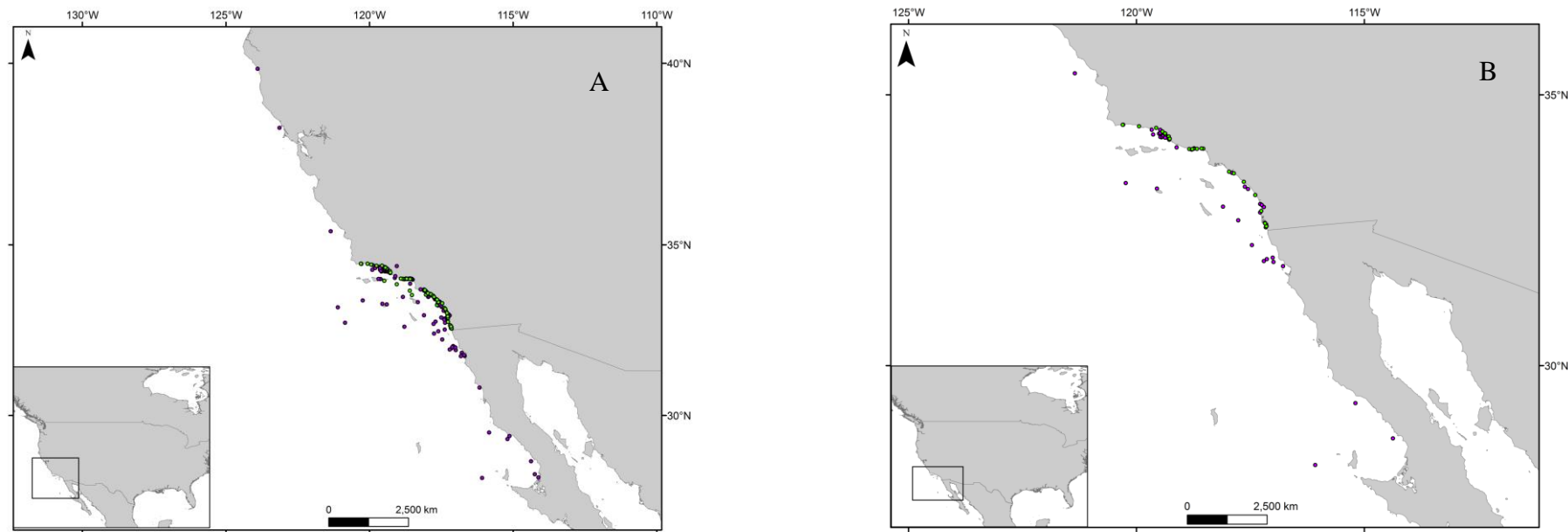


Figure 4: Maps showing tag and recapture locations for (A) all recaptured Common Thresher sharks (*Alopias vulpinus*) (1983-2015), $n = 105$ and (B) OTC tagged and recaptured Common Threshers whose vertebrae were used in this study ($n= 37$). Green dots are tagging locations and purple dots represent recapture locations.

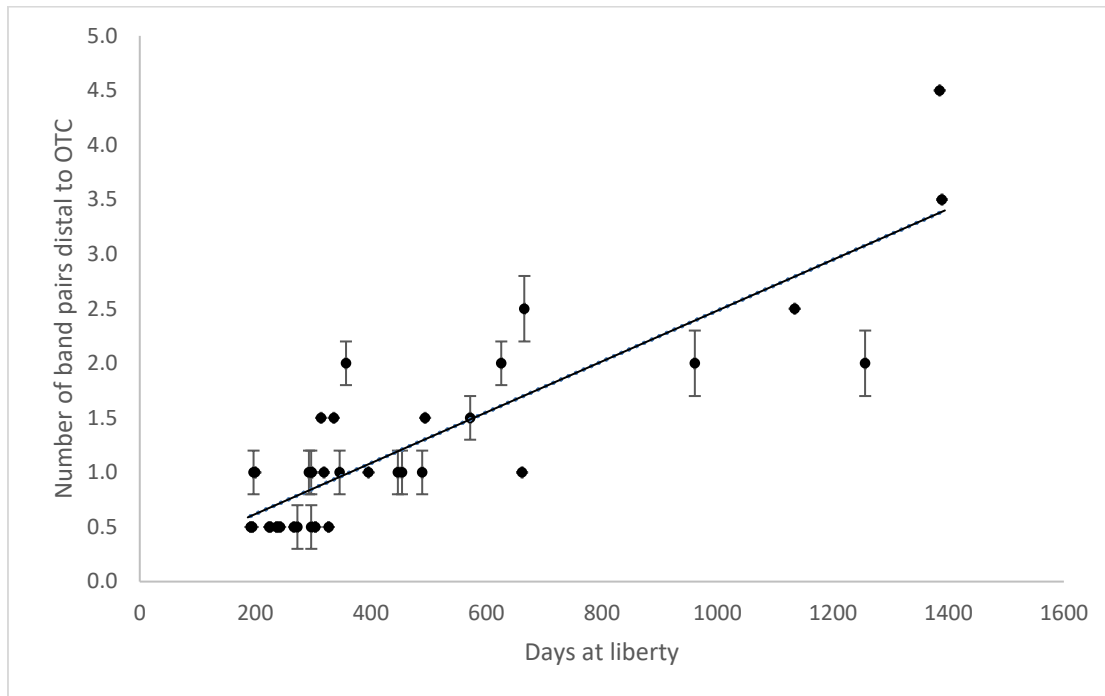


Figure 5: Average number of vertebral band pairs after the oxytetracycline mark compared to days at liberty. Common Threshers (*Alopias vulpinus*) tagged and recaptured in the northeastern Pacific (1998-2013). Readings were determined by 3 independent readers (\pm standard error [SE]). The solid line represents the linear regression of band pairs relative to days at liberty. Animals at liberty ≥ 0.5 years are included, $n=37$.

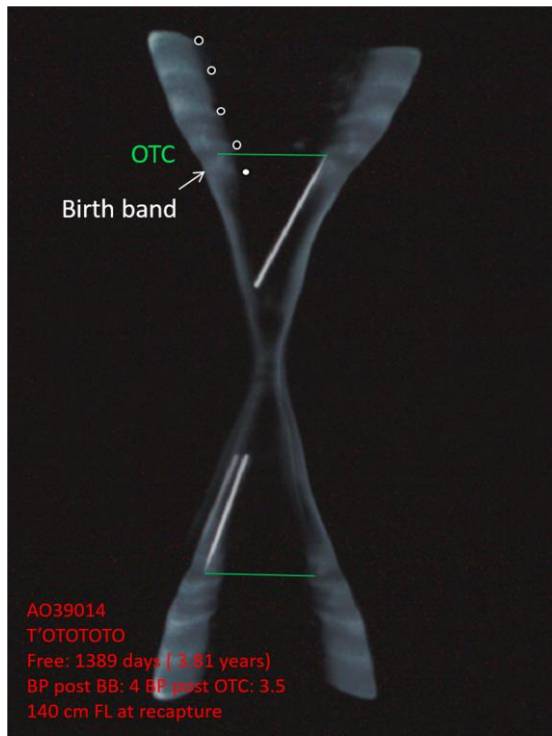


Figure 6: Band pair progression in X-ray images of a vertebra section showing band pair progression of an OTC-marked Common Thresher (*Alopias vulpinus*) recaptured in the northeastern Pacific Ocean. Translucent cartilage (dark bands on image) contrasted with more densely mineralized cartilage tissue (appearing light on image) shown with a “o” symbol to indicate the location of an opaque bands.

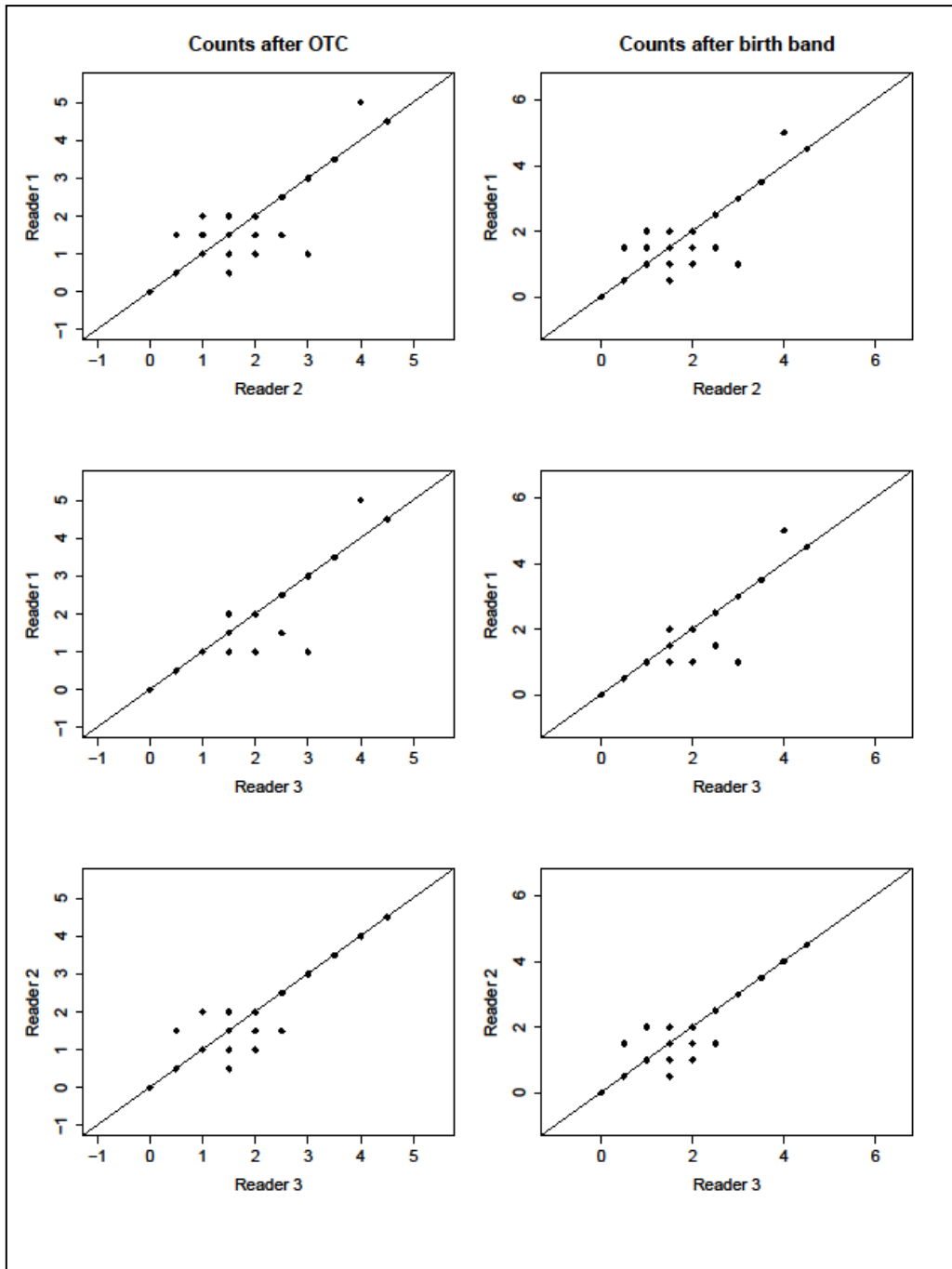


Figure 7: Age-bias plots for 3 independent readers who aged all OTC-marked Common Thresher (*Alopias vulpinus*) vertebrae to determine number of band pair counts distal to the OTC mark (left column) and total number of band pairs distal to the birth band (right column). No significant difference among band pair counts distal to the OTC mark (ANOVA; $P=0.998$) or among total counts distal to the birth band (ANOVA; $P=0.998$).

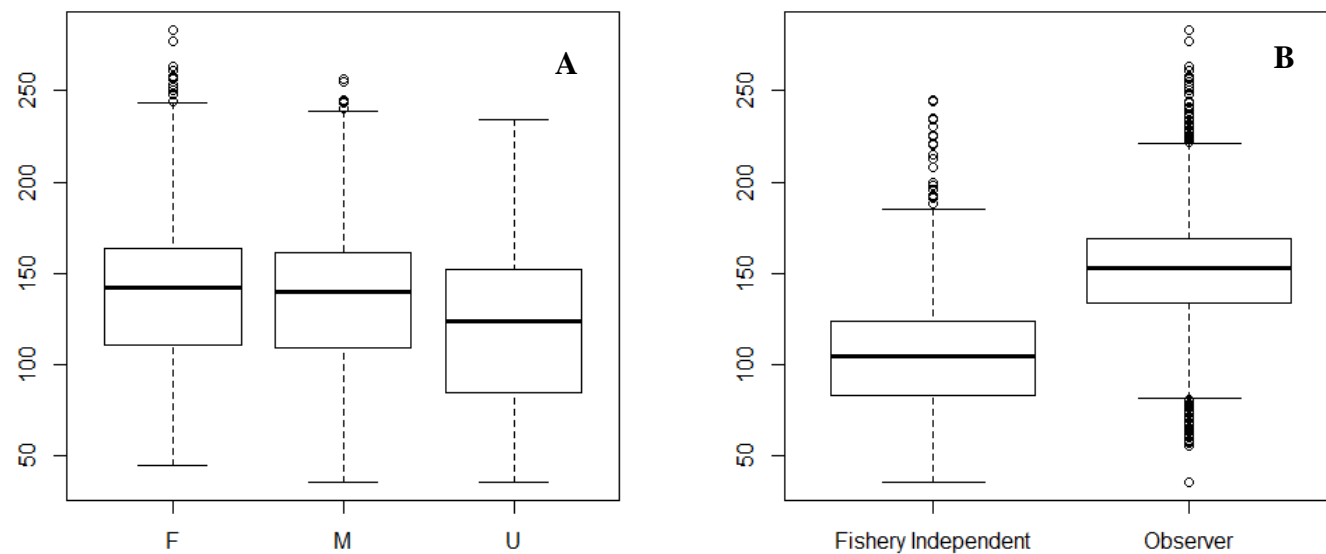


Figure 8: Boxplots showing (A) length distribution of male ($n= 3985$, fork length (FL) = $136 (\pm 0.57$ standard error [SE]), 36-256 cm) and female ($n= 4374$, FL = $138 (\pm 0.54$ SE), 45-283 cm) Common Threshers and (B) average length of fishery-independent ($n= 2488$, FL = $106 (\pm 0.53$ SE), 44-245 cm) and California drift gillnet and set net fishery observer data ($n= 5977$, FL = $149.5 (\pm 0.41$ SE), 36-283 cm) 1990-2014. Y-axes represent shark size in cm FL.

APPENDIX B:

TABLES

Table 1: Time required for oxytetracycline incorporation with vertebral tissue.....55

Table 2: Summary table of OTC-marked vertebrae samples from Common Thresher sharks (*Alopias vulpinus*) tagged and recaptured from 1998 to 2013 and at liberty ≥ 0.5 in the northeastern Pacific Ocean and included in this study. NMFS tag number, tag date, recapture date, fish length and sex are included, and number of band pairs (average of readings by independent readers) after (later in time) the OTC mark and birth band (± 1 standard error [SE]) are included in the table. Samples are sorted by time (days) at liberty. NL=either no length estimate provided by recapture party or length provided was unreliable, *=fork length (FL) was converted from total length or alternate length (origin of the first dorsal fin to the origin of the second dorsal) using the length regressions provided in the current study, +=measurement was converted from in to cm.56

Table 3: Methods used in previously published studies that include band pair counting of Common Thresher (*Alopias vulpinus*) vertebrae are not consistent. Vertebrae readers in the current study used a coding system to record the vertebral band pattern. In this code, O represents the term “opaque” and refers to bands that are denser than their translucent (T) counterparts. Opaque bands appear lighter in negative X-rays, darker in positive X-rays, and darker in reflected light. BB = birth band, and BP = band pair. The Example Reading column applies the count method from the respective study to the current study’s coding system for comparison of how the same vertebra would be interpreted in each respective study. Northeastern Pacific (NEPO) and western north Atlantic (WNA) studies are included. Counting technique details verified via personal communications (e-mail) with S. Smith and B. Gervelis, October 2016).....58

Table 1: Time required for oxytetracycline incorporation with vertebral tissue.			
Study	OTC injection Location	Species	Time to OTC mark Visibility
Tanaka 1990	Abdomen	Swell Shark (<i>Cephaloscyllium ventriosum</i>)	28 th day
Gruber & Stout 1983	Intramuscular	Lemon Sharks (<i>Negaprion brevirostris</i>)	Within 30 days
Smith 1984	Intraperitoneal cavity	Leopard Shark (<i>Triakis semifasciata</i>)	Within 30 days
Branstetter 1987	Intraperitoneal cavity	Blacktip Shark (<i>Carcharhinus limbatus</i>) and Atlantic Sharpnose Shark (<i>Rhizoprionodon terraenovae</i>)	36-72 days

<p>Table 2: Summary table of OTC-marked vertebrae samples from Common Thresher sharks (<i>Alopias vulpinus</i>) tagged and recaptured from 1998 to 2013 and at liberty ≥ 0.5 in the northeastern Pacific Ocean and included in this study. NMFS tag number, tag date, recapture date, fish length and sex are included, and number of band pairs (average of readings by independent readers) after (later in time) the OTC mark and birth band (± 1 standard error [SE]) are included in the table. Samples are sorted by time (days) at liberty. NL=either no length estimate provided by recapture party or length provided was unreliable, *=fork length (FL) was converted from total length or alternate length (origin of the first dorsal fin to the origin of the second dorsal) using the length regressions provided in the current study, + =measurement was converted from in to cm.</p>								
Fish ID	Time at liberty (days)	Tagging date	Recapture date	Sex	Length at tagging (cm FL)	Length at recapture (cm FL)	Number of band pairs after the OTC mark (± 1 SE)	Number of band pairs after the birth band (± 1 SE)
A039014	1389	9/7/2006	6/27/2010	M	80	140+	3.5 (0.0)	4.0 (0.0)
A039063	1385	9/9/2006	6/25/2010	F	85	142*	4.5 (0.3)	4.5 (0.3)
A079061	1256	9/13/2009	2/20/2013	F	101	115	2.0 (0.0)	3.0 (0.0)
A039565	1134	9/5/2007	10/13/2010	F	113	165+	2.5 (0.3)	3.5 (0.7)
A039019	961	9/7/2006	4/25/2009	F	83	NL	2.0 (0.3)	2.0 (0.0)
A079055	666	9/13/2009	7/11/2011	F	128	168+	2.5 (0.0)	5.0 (0.0)
A039543	662	9/7/2007	6/30/2009	F	105	NL	1.0 (0.2)	2.0 (0.0)
A039631	626	9/15/2007	6/2/2009	M	98	NL	2.0 (0.2)	3.5 (0.0)
A040636	572	9/18/2008	4/13/2010	F	114	132+	1.5 (0.0)	2.0 (0.0)
A038148	494	9/13/2006	1/20/2008	M	108	128*+	1.5 (0.2)	2.0 (0.3)
A038470	489	8/16/2004	12/18/2005	M	85	128	1.0 (0.2)	2.0 (0.2)
A039569	454	9/5/2007	12/2/2008	M	98	NL	1.0 (0.2)	2.5 (0.0)
A032625	447	7/12/1998	10/2/1999	F	112	NL	1.0 (0.0)	2.5 (0.0)
A039069	396	9/9/2006	10/10/2007	M	101	112	1.0 (0.2)	2.5 (0.3)
A040854	357	9/5/2009	8/28/2010	F	104	120*+	2.0 (0.2)	2.5 (0.2)
A039009	346	9/7/2006	8/19/2007	M	78	99*+	1.0 (0.0)	1.5 (0.0)
A039552	336	9/1/2007	8/2/2008	M	74	NL	1.5 (0.0)	2.0 (0.0)
A040543	327	9/9/2008	8/2/2009	M	85	109+	0.5 (0.0)	0.5 (0.0)
A040898	319	9/5/2009	7/21/2010	M	103	108*+	1.0 (0.0)	2.5 (0.0)
A040684	314	9/19/2008	7/30/2009	F	116	137+	1.5 (0.0)	3.0 (0.0)
A039611	304	9/8/2007	7/8/2008	F	96	137+	0.5 (0.0)	1.0 (0.2)
A040422	298	9/5/2008	6/30/2009	M	63	83*+	1.0 (0.2)	2.0 (0.2)
A039570	297	9/5/2007	6/28/2008	F	98	110*+	0.5 (0.0)	1.5 (0.3)
A040555	297	9/12/2008	7/6/2009	M	84	107*+	1.0 (0.2)	1.5 (0.0)
A039036	293	9/7/2006	6/27/2007	F	82	107*+	1.0 (0.2)	1.5 (0.2)

Table 2 Continued								
Fish ID	Fish ID	Fish ID	Fish ID	Fish ID	Fish ID	Fish ID	Fish ID	Fish ID
A082113	273	9/20/2012	6/20/2013	F	116	128* ⁺	0.5 (0.0)	2.0 (0.0)
A079196	267	9/6/2009	5/31/2010	F	92	112* ⁺	0.5 (0.0)	2.0 (0.0)
A040621	243	9/15/2008	5/16/2009	M	117	129* ⁺	0.5 (0.0)	2.5 (0.3)
A079039	239	9/19/2009	5/16/2010	F	106	NL	0.5 (0.0)	2.0 (0.0)
A079120	237	9/18/2009	5/13/2010	M	104	NL	0.5 (0.0)	2.0 (0.0)
A040866	226	9/4/2009	4/18/2010	M	80	92*	0.5 (0.0)	0.5 (0.0)
A079062	224	9/13/2009	4/25/2010	F	125	137 ⁺	0.5 (0.0)	2.0 (0.3)
A039591	200	9/8/2007	3/26/2008	M	104	NL	1.0 (0.2)	2.5 (0.2)
A039056	197	9/8/2006	3/24/2007	F	118	133* ⁺	1.0 (0.0)	1.0 (0.0)
A039051	195	9/8/2006	3/22/2007	M	106	120	0.5 (0.0)	2.0 (0.0)
A039118	193	9/12/2006	3/24/2007	F	115	NL	0.5 (0.0)	2.0 (0.0)
A039637	192	9/16/2007	3/26/2008	F	88	NL	0.5 (0.0)	0.5 (0.0)

Table 3: Methods used in previously published studies that include band pair counting of Common Thresher (*Alopias vulpinus*) vertebrae are not consistent. Vertebrae readers in the current study used a coding system to record the vertebral band pattern. In this code, O represents the term “opaque” and refers to bands that are denser than their translucent (T) counterparts. Opaque bands appear lighter in negative X-rays, darker in positive X-rays, and darker in reflected light. BB = birth band, and BP = band pair. The *Example Reading* column applies the count method from the respective study to the current study’s coding system for comparison of how the same vertebra would be interpreted in each respective study. Northeastern Pacific (NEPO) and western north Atlantic (WNA) studies are included. Counting technique details verified via personal communications (e-mail) with S. Smith and B. Gervelis, October 2016).

Study	Region	Location of first band (nearest to focus) included in counts	Location of outermost band included in count	Visualization technique	Includes partial band pair?	Type of band that completes pair	Example Reading: Total band pair count	Notes
Cailliet et al. 1983	NEPO	Embryonic tissue + BB is first BP.	Marginal-most T band	Positive X-ray	No (Assumption based on published methods)	T	BB TOTOT =3 BB TOTO =2 BB TOT = 2	BB (opaque) is included in counts, counts may be rounded down to the nearest whole pair, which is completed by a translucent band.
Smith et al. 2008b	NEPO	BB	Marginal band tissues	Negative X-ray	Yes	T	BB TOTOT =3 BB TOTO =2.5 BB TOT = 2	Translucent band completes the pair. BB is considered the first opaque band and is included in in first band pair. Includes Cailliet et al (1983) and additional samples. Cailliet et al. (1983) samples were not re-counted, though lengths were recalculated based on updated AL to TL conversion.
Gervelis & Natanson, 2013	WNA	First T band after BB	Final complete band pair, does not include marginal tissues if T.	Reflected light	No	O	BB TOTOT =2 BB TOTO =2 BB TOT = 1	Does not include partial band pairs. Does not include marginal tissue if transparent. Counts each opaque band after the birth band, therefore includes first translucent band after the BB within the total count.
Current study	NEPO	First T band after BB	Marginal band tissues	Negative X-ray	Yes	O	BB TOTOT =2.5 BB TOTO = 2 BB TOT = 1.5	Includes marginal tissue of either type as one band. Does not include BB.